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Intrinsic Parent-Offspring Correlation in Inbreeding Level in a Song Sparrow (*Melospiza melodia*) Population Open to Immigration

Jane M. Reid,^{1,*} Peter Arcese,^{2,†} and Lukas F. Keller^{3,‡}

1. School of Biological Sciences, Zoology Building, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, United Kingdom;

2. Centre for Applied Conservation Research, Forest Sciences, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia V6T 1Z4, Canada;

3. Zoologisches Museum, Universität Zürich, Winterthurerstrasse 190, 8057 Zürich, Switzerland

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ABSTRACT: The extent to which offspring resemble their parents in genotype and phenotype underpins patterns of genetic and phenotypic variation, selection, and evolution in natural populations. Genetic and phenotypic resemblance can clearly result from additive genetic variance and can be shaped by nongenetic parental and common environmental influences. In contrast, there is no straightforward expectation that inbreeding coefficient (f), a nonadditive component of genetic “quality,” should be correlated across parents and offspring in sexually reproducing species or consequently cause resemblance across generations. Here, we report a significant parent f -offspring f correlation within a free-living pedigreed population of song sparrows (*Melospiza melodia*) on Mandarte Island, Canada. Across 15 years, relatively inbred parents had relatively inbred offspring on average. We show that rather than requiring nonrandom pairing with respect to f and kinship, parent f -offspring f correlations arise as an intrinsic consequence of random pairing within Mandarte’s open population, where immigrants interbreed with Mandarte-hatched natives. However, on Mandarte, parent f -offspring f correlations may have been exacerbated because relatively inbred individuals paired with more closely related mates than expected by chance. Such intrinsic parent f -offspring f correlations have major implications for the understanding of resemblance, selection, and evolution in natural populations.

Keywords: good genes, heritability, heterozygosity, inbreeding depression, nonadditive genetic quality, phenotypic variation.

Knowledge of the extent to which offspring resemble their parents with respect to genotype and phenotype is critical to understanding patterns of genetic and phenotypic variation, selection, and evolution in natural populations (Schluter and Gustafsson 1993; Lynch and Walsh 1998; Merilä et al. 2001; Kruuk 2004). For example, the magnitude and mechanism of parent-offspring resemblance bears on the expected genetic and phenotypic response to natural selection and therefore the course of evolutionary change (Falconer and Mackay 1996; Merilä et al. 2001; Kruuk 2004) and on the evolutionary mechanisms driving and maintaining sexual selection (Wedell and Tregenza 1999; Kokko et al. 2003; Neff and Pitcher 2005). Quantifying the magnitude of parent-offspring resemblance within natural populations and understanding the mechanisms causing such resemblance are therefore key aims of evolutionary ecology (Lynch and Walsh 1998; Merilä et al. 2001; Kruuk 2004).

One major source of genetic and phenotypic resemblance among parents and offspring is clearly the direct inheritance of alleles with additive effects (Falconer and Mackay 1996; Lynch and Walsh 1998). Most empirical studies aiming to apportion phenotypic variance observed among relatives focus on quantifying the contribution of such additive genetic effects while controlling for nongenetic parental and common environmental influences (Norris 1993; Falconer and Mackay 1996; Griffith et al. 1999; Kruuk 2004; McCleery et al. 2004; Birkhead et al. 2005). A trait’s heritability (h^2 , the ratio of additive genetic variance to total phenotypic variance) often attracts particular attention, since h^2 predicts the expected evolutionary response to selection (Falconer and Mackay 1996; Lynch and Walsh 1998).

However, phenotypic variation can also be caused by nonadditive genetic dominance effects, reflecting heterozygosity at individual loci (e.g., Penn et al. 2002) and an

* Corresponding author; e-mail: jane.reid@abdn.ac.uk.

† E-mail: peter.arcese@ubc.ca.

‡ E-mail: lukas.keller@zoolmus.unizh.ch.

individual's inbreeding level or relative genome-wide heterozygosity (Falconer and Mackay 1996; Keller and Waller 2002). In particular, phenotypes often deteriorate markedly with inbreeding because of increased expression of deleterious recessive alleles and reduced expression of overdominance with increased homozygosity (Charlesworth and Charlesworth 1987; Keller and Waller 2002). Such nonadditive genetic effects can clearly contribute to genetic and phenotypic resemblance among full siblings, since full siblings share the same inbreeding level and a substantial proportion of autosomal genotypes (Falconer and Mackay 1996). However, nonadditive genetic attributes are not transmitted directly from parents to offspring in sexually reproducing species; offspring inherit their parents' genes but not their genotypes (Falconer and Mackay 1996). There is therefore no straightforward expectation that inbreeding level should be correlated across parents and offspring. For example, both inbred and outbred parents could pair with closely related or unrelated mates, thereby producing either inbred or outbred offspring. Consequently, empirical studies of parent-offspring resemblance typically do not consider whether phenotypic resemblance observed across generations might reflect correlated inbreeding effects as well as additive genetic, nongenetic parental, and environmental components (Norris 1993; Kruuk 2004; McCleery et al. 2004). Similarly, it is often assumed that choosy individuals cannot produce outbred offspring by choosing outbred mates (as opposed to dissimilar mates; Mays and Hill 2004). A general mechanism of parent-offspring resemblance with respect to inbreeding level would therefore constitute an additional force of genetic and phenotypic resemblance across generations, with wide-ranging implications for the understanding of selection and evolution in natural populations.

Here, we report a marked parent-offspring correlation in inbreeding coefficient (f) within a pedigreed population of song sparrows (*Melospiza melodia*) on Mandarte Island, Canada. Across 15 years, relatively inbred males and females had relatively inbred offspring on average. This implies a parent-offspring correlation in relative genome-wide heterozygosity, a nonadditive component of genetic "quality" (Neff and Pitcher 2005). We investigate how this correlation arose.

First, we investigate whether relatively inbred song sparrows were more closely related to the set of potential mates than were outbred sparrows and were therefore more likely to produce inbred offspring simply given random pairing. Such a relatedness structure might arise within an open population such as Mandarte's song sparrows, where immigrant breeders pair with locally hatched natives to produce relatively outbred offspring. Outbred individuals might consequently be relatively likely to carry recent im-

migrant alleles and therefore to be relatively unrelated to most existing population members.

Second, we investigate whether parent f -offspring f correlations observed on Mandarte were exacerbated by nonrandom inbreeding with respect to individual f . Specifically, we test whether relatively inbred song sparrows paired with closer relatives than expected under random pairing (and therefore produced relatively inbred offspring), while outbred sparrows paired with less closely related mates than expected (and therefore produced relatively outbred offspring). Such patterns of nonrandom inbreeding might arise if inbreeding directly depresses the ability to avoid kin, or they might reflect state-dependent constraints or variation in optimal mate choice among related individuals.

Finally, we investigate whether parent f -offspring f correlations were further exacerbated because immigrants to Mandarte (which produce relatively outbred offspring when paired with Mandarte-hatched natives) paired with more outbred natives than expected by chance. We consider the likely generality of the parent f -offspring f correlations observed on Mandarte and discuss the implications for the understanding of parent-offspring resemblance, selection, and evolution in natural populations.

Methods

Study Population

Mandarte Island, ≈ 6 ha in size, lies 25 km northeast of Victoria, British Columbia, Canada. Its resident song sparrow population has been studied intensively since 1975 and has fluctuated between four and 74 breeding pairs during this time (Smith et al. 2006). Every song sparrow fledged on Mandarte has been individually color-banded in the nest or soon after fledging (Smith et al. 2006). Unbanded immigrants to the breeding population can therefore be distinguished from Mandarte-hatched natives and have themselves been individually color-banded soon after they settled (Marr et al. 2002; Smith et al. 2006). All population members are therefore individually identifiable. Mandarte lies within 5 km of numerous other islands, including Vancouver Island (31,300 km²), and numerous unbanded song sparrows pass through Mandarte outside of the breeding season. However, although song sparrows fledged elsewhere can clearly reach Mandarte, relatively few immigrants settle there to breed (average of 1.1/year since 1976; Smith et al. 2006).

Song sparrows on Mandarte can breed from ages of 1 to 8 years, although most recruits survive only 1–3 years (Smith et al. 2006). Individuals commonly remain with the same mate across years, but both sexes remate if their original mate dies, and some individuals switch between

living mates within and among seasons (Arcese 1989; Smith et al. 2006). Each spring since 1975, all song sparrows alive on Mandarte have been identified. All social pairings where breeding was attempted and all territorial males that remained unmated have been documented (Arcese 1989; Smith et al. 2006). A complete population pedigree, covering all individuals hatched since 1981, has been compiled from observed social pairings (Keller 1998).

Pedigree Analyses

We calculated individual inbreeding coefficients (f) and kinship coefficients between male-female pairs (k) directly from the pedigree using standard algorithms (Falconer and Mackay 1996). The value of f reflects the probability that two homologous alleles will be identical by descent and predicts an individual's genome-wide homozygosity relative to a baseline population (Wright 1922; Falconer and Mackay 1996; table 1). The value of k reflects the relatedness between any male-female pair and equals the f of offspring produced by that pairing (Wright 1922; Falconer and Mackay 1996; table 1). Immigrants to Mandarte are generally of unknown parentage and therefore have unknown f . However, immigrants generally do not originate from immediately adjacent islands where resident song sparrows are also color-banded (Marr et al. 2002). Furthermore, immigrants are genetically distinguishable from Mandarte's native population at the time of arrival (assignment test based on nine microsatellite loci; $P < .02$ for all immigrants during 1994–1997; see also Keller et al. 2001). The first-generation (F1) offspring of immigrant-native pairings can therefore be defined as outbred relative to Mandarte's baseline population ($f = 0$; Keller 1998; Marr et al. 2002; see also van Tienderen and van Noordwijk 1988). Immigrants can, however, produce inbred offspring in subsequent generations by pairing with their own

descendants. Since extrapair fertilizations (EPFs) occur on Mandarte (O'Connor et al. 2006), the pedigree contains paternity errors. However, there is no evidence that EPFs occur systematically with respect to f or k (Keller and Arcese 1998; O'Connor et al. 2006). The EPFs therefore introduce error but not bias into estimates of f and k (Keller and Arcese 1998; see also Keller et al. 2002; Kruuk et al. 2002). Despite this error, pedigree-based estimates of f are likely to be more accurate than estimates derived from small numbers of molecular markers (Slate et al. 2004). Pedigree-based methods also allow k to be calculated for any hypothetical male-female pairing, irrespective of whether those individuals actually paired or produced offspring.

The coefficient f measures inbreeding relative to an arbitrary baseline population, typically defined as the population of individuals alive at the start of a study (Falconer and Mackay 1996; Keller and Waller 2002). Mean f therefore increases through initial pedigree generations before stabilizing (given sufficient immigration) because distant common ancestors contribute little to f (Falconer and Mackay 1996; Keller 1998). To reduce uncertainty associated with comparing f across individuals with known pedigrees of different lengths, we restricted current analyses to sparrows alive on Mandarte during 1990–2004. A population bottleneck in 1989 eliminated all individuals hatched before estimates of f stabilized (Keller 1998).

Parent f –Offspring f Correlations

We used general linear models to test whether offspring f varied with maternal f or paternal f . We also related offspring f to “midparent f ,” defined as the average of maternal f and paternal f across pairings where f was known for both parents (i.e., where neither parent was an immigrant). Midparent-offspring regression is a standard

Table 1: Definitions of terminology

Term	Definition
f	An individual's coefficient of inbreeding, reflecting the probability that any two homologous alleles will be identical by descent.
k	Kinship between a male-female pair, equal to the f of offspring produced by that pairing.
k_m	An individual's mean kinship with the set of potential mates, calculated under the all-mates and new-mates null models.
k_d	Difference between an individual's kinship with its observed social mate (k_{obs}) and its k_m , indicating the degree to which an individual paired with a more or less closely related mate than expected by chance.
f_m	Mean f of an immigrant's set of potential mates, calculated under the all-mates and new-mates null models.
f_d	Difference between the f of an immigrant's observed social mate (f_{obs}) and its f_m , indicating the degree to which an immigrant paired with a more or less inbred mate than expected by chance.

method of quantifying resemblance between parents and progeny with respect to quantitative phenotypic traits (Falconer and Mackay 1996). Since f is not an additive genetic quantity, the gradient of a midparent f -offspring f regression cannot be interpreted as a strict heritability, but it does allow effect sizes to be compared with those reported for quantitative traits elsewhere. We repeated analyses across all song sparrow pairings observed during 1990–2004 (modeling “year” as a factor) and across all pairings observed in each individual year. Pairs that remained together over multiple years were included in overall analyses only once, in the year in which they formed. Of individual females and males (rather than pairings), 48% and 46%, respectively, were included more than once because they paired with more than one mate during their lifetimes. However, no individual contributed >2% of all observations, and results were qualitatively identical when analyses were repeated using a single randomly chosen pairing per individual.

Null Models of Kinship

It is notoriously difficult to test whether mating patterns occurring within natural populations are biased with respect to specific traits. Rigorous analyses require the correct null model of mate availability to be specified. This in turn requires the set of potential mates available to each focal individual and their respective trait values to be accurately known (van Tienderen and van Noordwijk 1988; Pärt 1996; Keller and Arcese 1998). Such analyses are more tractable in Mandarte’s song sparrows than in most natural populations, since the identity and mating status of all population members is known in each year. However, since pairs establish in an unknown order, mate availability still cannot be quantified exactly. Furthermore, since song sparrows occasionally switch mates and mate polygamously (Smith et al. 2006), observing that a monogamous pair remained together does not prove that paired individuals had not been available for further pairing. We therefore used two different null models to test whether an individual’s kinship (k) with its potential or actual mates varied, or varied nonrandomly, with its inbreeding coefficient (f). First, we derived an “all-mates” model, where the set of potential mates available to each focal individual comprised all opposite-sex individuals alive on Mandarte in a focal year (thus quantifying an individual’s k with the entire opposite-sex population, irrespective of their current or previous pairing status). Second, we derived a “new-mates” model, where the set of potential mates available to each individual was restricted to all opposite-sex individuals that had definitely been available for pairing during a focal year (namely, new recruits to the breeding population, individuals that had switched

mates since the previous year, and territorial males that remained unmated). The few nonterritorial “floater” males were not included as potential mates because floaters rarely acquire social mates or EPFs on Mandarte (Arcese 1989; O’Connor et al. 2006). Similar all-mates and new-mates null models were used in previous analyses of inbreeding avoidance on Mandarte (Keller and Arcese 1998). These two null models occupy opposite ends of the likely spectrum of true mate availability, and we surmised that results that remain consistent under both models are likely to be robust. A null model that incorporated spatial information could additionally have been derived. This would be necessary to avoid biases if song sparrows settled close to relatives and moved relatively short distances when switching mates. However, within Mandarte, song sparrows do not settle closer to or further from their natal territory or siblings than expected by chance (Arcese 1989). Furthermore, individuals that switch mates can move across the island rather than solely to neighboring territories (Smith et al. 2006). There is therefore no biological reason to consider spatially constrained null models within the small spatial context of Mandarte.

Individual f and Kinship

For every song sparrow recruited on Mandarte during 1990–2004, we identified the set of potential mates available in each year under the all-mates and new-mates null models. We then used the population pedigree to calculate k for every potential pairing and described the distribution of k for each focal individual under each null model for each year. We used mean k (k_m ; table 1) as our primary measure of an individual’s kinship with the set of potential mates. All results were qualitatively similar when analyses were repeated using median k . To determine whether relatively inbred individuals were more closely related to the set of potential mates than were outbred individuals, we tested whether k_m was positively correlated with f across individuals. We repeated analyses across all individuals recruited on Mandarte during 1990–2004 and across all individuals alive in each individual year. Individuals that survived multiple years were included in overall analyses only once, with k_m calculated from the sets of potential mates in the individual’s first possible breeding season (1 year of age). Results were quantitatively similar if each individual was included in each year in which it paired with a new mate.

We then used simulations in which each individual was randomly allocated a mate from those available under each null model to estimate the magnitude of the parent f -offspring f correlation that would have arisen on Mandarte under random pairing. First, we allocated one random mate to each male and female recruited on Mandarte dur-

ing 1990–2004. Second, we allocated the same number of random mates to each individual as the number with which it actually paired during each year. We used the Mandarte pedigree to calculate offspring f for each randomized pairing and related offspring f to parental f across all pairings. The mean parent f –offspring f correlation that would have arisen under random pairing was estimated over 5,000 iterations of this process.

Nonrandom Inbreeding

We used two approaches to test whether inbreeding occurred nonrandomly with respect to individual f (specifically, whether more inbred song sparrows paired with more closely related mates than expected by chance). First, we calculated a kinship difference score (k_d) for each song sparrow that recruited on Mandarte during 1990–2004, where k_d is the difference between an individual's kinship with its observed mate (k_{obs}) and its mean kinship with the set of potential mates (calculated under the all-mates and new-mates null models; thus, $k_d = k_{\text{obs}} - k_m$; table 1). Positive and negative k_d values, respectively, indicate that a focal individual paired with a more or less closely related mate than expected by chance. We then tested whether k_d was positively correlated with individual f across all observed pairings (as predicted if more inbred individuals paired with closer relatives than expected). We repeated analyses across all pairs formed during 1990–2004 and across all pairs formed in each individual year. Pairs that remained together over multiple years were included in overall analyses only once, with k_d calculated for the year in which the pair formed. Simulations supported our assumption of a null slope of 0 for the correlation between k_d and f .

Next, we used a more general, global approach to test whether song sparrows paired nonrandomly with respect to f and k . We used the population pedigree to calculate k for every possible male–female pairing that could have formed on Mandarte during 1990–2004, thus generating the entire distribution of k . We then tested whether the slope of the relationship between k and f across all possible pairings differed from the slope observed across pairings that actually formed (i.e., testing for an interaction between f and observed vs. possible pairings). A steeper slope across observed pairings than across all possible pairings would indicate that more inbred song sparrows paired with more closely related mates than expected under the null model of completely random pairing. Analyses were repeated for males and females separately so that each observed pairing was included only once.

Immigrants

Immigrant breeders were not included in the above analyses because f is unknown for immigrants. However, since offspring of immigrant–native pairings are considered outbred ($f = 0$), we investigated whether immigrants paired with more outbred mates than expected by chance (meaning that these outbred mates had outbred offspring). For each immigrant we calculated the difference (f_d) between the f of its mate (f_{obs}) and the mean f (f_m) of the immigrant's set of potential mates under the all-mates and new-mates null models (thus, $f_d = f_{\text{obs}} - f_m$; table 1). Positive and negative f_d values, respectively, indicate that an immigrant paired with a more or less inbred mate than expected by chance. We used one-sample t -tests to determine whether f_d differed from 0 across all immigrant–native pairings, with f_m calculated for the year in which each pair formed. Since some immigrants paired with multiple mates during their lifetimes, we repeated analyses using mean f_d averaged across all pairings involving each immigrant. Data from male and female immigrants were pooled because of small sample sizes.

Models used normal error structures. Where dependent variables and residuals departed from normality, we used randomization tests to verify whether test statistics differed significantly from 0 (Manly 1991). Dependent variables were resampled with replacement over 5,000 iterations (although all parameter estimates and associated P values in fact stabilized within 2,000 iterations). We used Spearman rank correlations for individual year analyses because of small sample sizes. In practice, hypothesis tests based on parametric, nonparametric, and randomization approaches gave qualitatively similar results. A small number of highly inbred pairings between siblings or between parents and offspring produced outlying data points. To investigate the influence of these pairings on parent f –offspring f correlations, we repeated analyses after excluding pairings where offspring $f \geq 0.25$. Quadratic f^2 terms were included in models where inspection suggested nonlinear relationships. Terms were retained if $P < .1$. All tests were two tailed. We used one-sample Kolmogorov–Smirnov tests to determine whether distributions of variables or residuals departed from normality. We applied sequential Bonferroni corrections where tests were repeated across each of 15 years (Sokal and Rohlf 2001), although nonsignificant correlations may consequently reflect low statistical power rather than necessarily small effect sizes (Nakagawa 2004). Pedigree analyses were run in Pedigree Viewer (<http://www-personal.une.edu.au/~bkinghor/pedigree.htm>). Statistical analyses and simulations were run in SPSS (ver. 14.0), Microsoft Excel, and R (ver. 1.8.1).

Results

Across 375 Mandarte-hatched song sparrows recruited on Mandarte during 1990–2004, f varied from 0.000 to 0.305 (median = 0.044). Across 358 observed pairings (including those involving 15 immigrant breeders), k varied from 0.000 to 0.357 (median = 0.064). Distributions of f and k were positively skewed (skewness: 1.86 ± 0.13 and 1.76 ± 0.13 , respectively) and differed from normality (all $P < .001$). Neither f nor k increased across years ($r = 0.06$, $N = 375$, $P = .23$; and $r = -0.06$, $N = 358$, $P = .26$, respectively).

Parent f –Offspring f Correlations

Across all pairings, offspring f was positively correlated with maternal f , paternal f , and midparent f (fig. 1). Maternal f was weakly correlated with paternal f ($r = 0.11$, $N = 319$, $P = .06$). Effect sizes increased slightly when highly inbred pairings were excluded ($r = 0.32$, $N = 318$, $P < .001$; $r = 0.36$, $N = 333$, $P < .001$; and $r = 0.46$, $N = 303$, $P < .001$ for correlations between offspring f and maternal f , paternal f , and midparent f , respectively).

Parent f –offspring f correlations remained significant after we controlled for year (table 2), and offspring f was to some degree correlated with maternal f , paternal f , and midparent f in all 15 individual years (table 2). Therefore, on Mandarte, relatively inbred song sparrows consistently had relatively inbred offspring on average.

Individual f and Kinship

Across all Mandarte-hatched song sparrows recruited on Mandarte during 1990–2004, k_m averaged 0.079 and 0.081 for females ($N = 181$) and 0.076 and 0.079 for males ($N = 194$) under the all-mates and new-mates null models, respectively (standard deviation ≈ 0.023 in all cases). For both sexes, k_m was approximately normally distributed under both null models and varied 14-fold among individuals (from 0.011 to 0.150).

In both females and males, k_m was positively correlated with f under both null models (females: $N = 181$, $r = 0.39$, $P < .001$; and $r = 0.44$, $P < .001$; males: $N = 194$, $r = 0.53$, $P < .001$; and $r = 0.46$, $P < .001$ under the all-mates and new-mates models, respectively; fig. 2). Relationships remained significant after we controlled for year, and quadratic f^2 terms were significant in all four analyses (table 3; fig. 2). However, k_m did not decline with f beyond the algebraic maximum (all $P > .15$), indicating that k_m leveled off rather than declining across highly inbred individuals. In all 15 individual years, k_m was to some degree correlated with f in both sexes under both null models (table 3). Therefore, on Mandarte, relatively inbred song

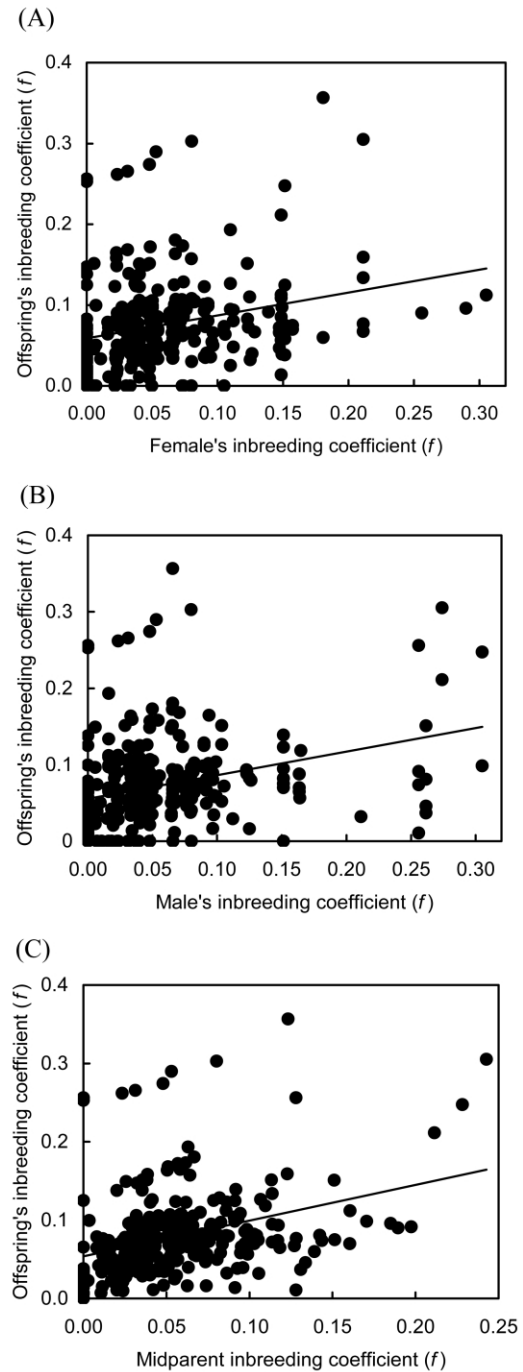


Figure 1: Relationships between offspring inbreeding coefficient (f) and (A) maternal f , (B) paternal f , and (C) midparent f across all song sparrow pairings observed on Mandarte during 1990–2004. Offspring f was positively correlated with maternal f , paternal f , and midparent f ($r = 0.24$, $N = 330$, $P < .001$; $r = 0.29$, $N = 345$, $P < .001$; and $r = 0.34$, $N = 315$, $P < .001$, respectively). The value of N differs from the total sample of 358 pairings because some males and females were immigrants (and therefore of unknown f).

Table 2: Relationships between offspring inbreeding coefficient (f) and maternal f , paternal f , and midparent f across all song sparrow pairings observed on Mandarte during 1990–2004 and across all pairings observed in each individual year

	Maternal f			Paternal f			Midparent f		
	N	F or r_s	P (η^2)	N	F or r_s	P (η^2)	N	F or r_s	P (η^2)
Relationships for all pairings observed during study:									
Parent f	330	12.4	.001 (.03)	345	32.3	.001 (.09)	315	9.2	.003 (.03)
Year		1.3	.18		1.1	.37		1.9	.03
Year \times parent f		2.4	.004 (.09)		.9	.54 (.03)		2.7	.001 (.11)
Relationships for pairings observed in individual years:									
1990	10	.10	.78	13	.16	.59	10	.49	.15
1991	27	.25	.21	27	.22	.27	25	.28	.18
1992	41	.40	.01	46	.31	.029	39	.44	.005*
1993	48	.71	.001*	50	.49	.001*	46	.68	.001*
1994	58	.56	.001*	60	.27	.040	57	.41	.002*
1995	46	.48	.001*	47	.30	.041	45	.49	.001*
1996	47	.37	.012	47	.46	.001*	45	.51	.001*
1997	49	.36	.011	49	.60	.001*	48	.64	.001*
1998	37	.05	.77	39	.47	.003*	35	.47	.004*
1999	13	.20	.51	13	.51	.072	12	.46	.13
2000	16	.42	.11	15	.59	.021	14	.71	.004*
2001	14	.33	.25	15	.14	.62	12	.71	.009*
2002	26	.52	.007	26	.31	.13	23	.74	.001*
2003	28	.37	.056	28	.57	.002*	26	.70	.001*
2004	17	.55	.022	18	.53	.022	17	.79	.001*

Note: F ratios and Spearman correlation coefficients (r_s) are presented for overall and individual year analyses, respectively. The value of N differs among analyses within each year because some males and females were immigrants (and of unknown f). The value of N for overall analyses does not equal the sum of N across individual years because overall analyses included individual pairs only once, even if they survived multiple years.

Values of η^2 for main and interactive effects of f are shown in parentheses (effect sizes can therefore be estimated as η).

* Spearman correlation significant at $\alpha = 0.05$ after sequential Bonferroni correction for 15 tests of each hypothesis.

sparrows were on average more closely related to the set of potential mates than were relatively outbred song sparrows. Simulations confirmed that substantial parent f –offspring f correlations would arise, assuming a single random pairing involving each female and male recruited on Mandarte during 1990–2004 (maternal f : $r = 0.15$, $N = 181$, $P = .042$; paternal f : $r = 0.17$, $N = 194$, $P = .014$) and assuming a distribution of pairings matching that observed for each female and male (maternal f : $r = 0.15$, $N = 330$, $P = .005$; paternal f : $r = 0.19$, $N = 345$, $P < .001$).

Individual f and Nonrandom Pairing

Across all observed pairings comprising Mandarte-hatched song sparrows, k_d varied from -0.13 to 0.27 . Consistent with previous analyses that found no evidence of overall inbreeding avoidance in song sparrows on Mandarte (Keller and Arcese 1998), mean k_d did not differ from 0 for either sex under either null model (all $P > .1$). Distributions of k_d were positively skewed (skewness: 1.7 ± 0.13

for both sexes under both null models) and differed from normality (all $P < .001$).

In both females and males, k_d was weakly positively correlated with f under both null models (females: $N = 330$, $r = 0.12$, $P = .035$; and $r = 0.10$, $P = .086$; males: $r = 0.12$, $N = 345$, $P = .031$; and $r = 0.12$, $P = .026$ under the all-mates and new-mates models, respectively). Typically, k_d was negative in outbred individuals ($f = 0$; mean $k_d \leq -0.005$) and positive in relatively inbred individuals ($f \geq 0.125$; mean $k_d \geq 0.008$) under both null models, indicating that outbred and inbred individuals respectively paired with marginally less closely and more closely related mates than expected. However, f explained a small proportion of variation in k_d ($< 2\%$ in all cases).

Overall relationships between f and k_d remained significant for males but not females after we controlled for year, but they varied among years in females but not males (table 4). Also, k_d was not significantly correlated with f in any individual year in either sex under either null model ($r_s \leq 0.55$, $P \geq .1$ in all cases after Bonferroni correction).

The gradient of the relationship between f and k was

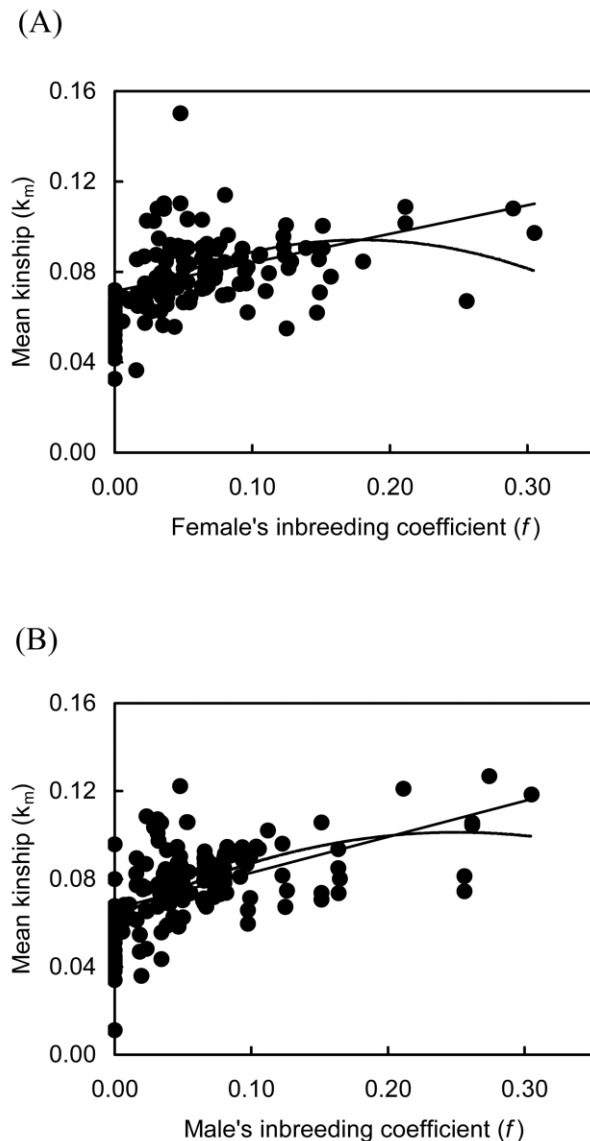


Figure 2: Relationships between an individual's inbreeding coefficient (f) and its mean kinship (k_m) with the set of possible mates for (A) all female and (B) all male song sparrows recruited on Mandarte during 1990–2004. In both females and males, k_m increased with f (table 3). Both linear and quadratic regression lines are shown (data from the all-mates null model).

marginally steeper across song sparrow pairings observed on Mandarte during 1990–2004 than across all possible pairings for males ($b = 0.29$ vs. $b = 0.15$, $P = .05$) but not for females ($b = 0.24$ vs. $b = 0.15$, $P = .10$).

Immigrants

Fifteen immigrants bred on Mandarte during 1990–2004 (three males and 12 females). These immigrants did not

pair with more outbred mates than expected by chance across all observed immigrant-native pairings ($N = 33$; all-mates: $t = -0.8$, $df = 32$, $P = .46$; new-mates: $t = -1.0$, $df = 32$, $P = .32$) or on average across all pairings involving each individual immigrant ($N = 15$; all-mates: $t = -1.2$, $df = 14$, $P = .27$; new-mates: $t = -1.6$, $df = 14$, $P = .12$). However, analyses were sensitive to one pairing where an immigrant female paired with an inbred male for one breeding attempt ($f_d = 0.11$). With this pairing excluded, immigrants tended to pair with more outbred mates than expected across all pairings ($N = 32$; all-mates: $t = -1.8$, $df = 31$, $P = .09$; new-mates: $t = -2.0$, $df = 31$, $P = .05$) and on average across all pairings involving each immigrant ($N = 15$; all-mates: $t = -1.9$, $df = 14$, $P = .08$; new-mates: $t = -2.3$, $df = 14$, $P = .04$).

Discussion

The extent to which offspring resemble their parents in genotype and phenotype is a key issue in evolutionary ecology (Schluter and Gustafsson 1993; Merilä et al. 2001). Phenotypic resemblance can clearly result from additive genetic variance and from maternal and common environmental effects (Schluter and Gustafsson 1993; Kruuk 2004). In contrast, it is often assumed that nonadditive genetic attributes, such as an individual's inbreeding level, will not be correlated across parents and offspring and therefore do not contribute to genetic or phenotypic resemblance across generations (Falconer and Mackay 1996; Mays and Hill 2004). In song sparrows on Mandarte, an offspring's coefficient of inbreeding (f) was positively correlated with the inbreeding coefficient of its parents. The correlation observed across 15 years of natural pairings was not caused by temporal covariation in f across parents and offspring, and it held to some degree in every individual year. Relatively inbred song sparrows therefore had relatively inbred offspring on average.

How did this parent f –offspring f correlation arise? Analyses of the Mandarte pedigree, based on two null models of mate availability, suggested that a song sparrow's kinship (k) with the set of potential mates increased with its own f . Relatively inbred sparrows were more closely related to the set of potential mates than were outbred sparrows, and they were therefore more likely to produce inbred offspring simply given random pairing. Further inspection suggested that this relatedness structure arose because inbred individuals were likely to be offspring of native Mandarte parents rather than recent immigrants and were therefore less likely to carry recent immigrant alleles. They were therefore relatively closely related to most other population members. Conversely, outbred individuals were relatively likely to have an immigrant in their recent an-

Table 3: Relationships between an individual song sparrow's inbreeding coefficient (f) and its mean kinship (k_m) with the set of potential mates under the all-mates and new-mates null models across all females and males alive on Mandarte during 1990–2004 and across all females and males alive in each individual year

	Females					Males				
	All-mates model			New-mates model		All-mates model			New-mates model	
	N	F or r_s	P (η^2)	F or r_s	P (η^2)	N	F or r_s	P (η^2)	F or r_s	P (η^2)
Relationships for all pairings observed during study:										
f	181	18.2	<.001 (.05)	27.4	<.001 (.08)	194	46.6	<.001 (.09)	21.1	<.001 (.08)
f^2		36.3	<.001 (.11)	47.1	<.001 (.14)		18.1	<.001 (.05)	16.9	<.001 (.07)
Year		3.4	.001	5.3	<.001		2.0	.02	1.9	.03
Year \times f		4.8	<.001 (.22)	4.5	<.001 (.17)		1.0	.50 (.05)	2.0	.02 (.11)
Relationships for pairings observed in individual years:										
1990	7	.74	.056	.74	.056	11	.45	.17	.45	.17
1991	25	.69	.001*	.81	.001*	23	.57	.005*	.58	.004*
1992	36	.68	.001*	.59	.001*	41	.57	.001*	.48	.001*
1993	39	.54	.001*	.56	.001*	47	.70	.001*	.66	.001*
1994	49	.63	.001*	.64	.001*	57	.68	.001*	.63	.001*
1995	39	.63	.001*	.72	.001*	47	.47	.001*	.37	.010
1996	44	.71	.001*	.87	.001*	46	.46	.002*	.40	.002*
1997	39	.56	.001*	.56	.001*	49	.61	.001*	.48	.001*
1998	27	.48	.011	.32	.10	37	.59	.001*	.57	.001*
1999	10	.21	.56	.43	.21	13	.32	.28	.34	.25
2000	13	.60	.029	.55	.051	15	.59	.021	.49	.066
2001	11	.49	.12	.85	.001*	14	.13	.66	.12	.68
2002	25	.69	.001*	.80	.001*	24	.39	.069	.47	.022
2003	26	.52	.007*	.54	.005*	27	.64	.001*	.73	.001*
2004	14	.37	.19	.37	.19	17	.82	.001*	.81	.001*

Note: F ratios and Spearman correlation coefficients (r_s) are presented for overall and individual year analyses, respectively. Values of η^2 for main and interactive effects of f are shown in parentheses.

* Spearman correlation significant at $\alpha = 0.05$ after sequential Bonferroni correction for 15 tests of each hypothesis.

cestry and therefore to carry recent immigrant alleles. They were therefore relatively unrelated to most other population members and would consequently produce relatively outbred offspring on average under random pairing. Specifically, 30 of 39 (>75%) pairings that produced outbred offspring ($f = 0$) during 1990–2004 included an immigrant parent, compared to one of 48 (2%) pairings that produced relatively inbred offspring ($f \geq 0.125$; Fisher's exact test, $P < .001$; one immigrant female paired with her grandson during her third year of residence). Observed parent f –offspring f correlations declined by 5%–10% if F1 offspring of immigrant breeders were excluded. Simulations in which individual sparrows were randomly allocated mates from those available under each null model confirmed that the intrinsic relatedness structure of Mandarte's song sparrow population is sufficient to generate a substantial parent f –offspring f correlation under random pairing.

A critical assumption underlying these analyses is that F1 offspring of immigrant-native pairings can be consid-

ered outbred relative to Mandarte's baseline population. This assumption is justified because immigrants to Mandarte are known to originate from many different source populations and can be reliably distinguished from existing residents based on microsatellite genotype (see the introduction to this article; Keller et al. 2001; Smith et al. 2006). In fact, the degree of genetic differentiation among local song sparrow populations exceeds that observed among recognized song sparrow subspecies in California (Chan and Arcese 2003). The parent f –offspring f correlation observed in the Mandarte pedigree is therefore likely to reflect a true parent–offspring correlation with respect to inbreeding level and relative genome-wide heterozygosity. Within Mandarte's open song sparrow population, offspring are therefore intrinsically likely to resemble their parents with respect to f and relative heterozygosity, a nonadditive component of genetic quality (Neff and Pitcher 2005).

It is difficult to test definitively whether parent f –offspring f correlations were exacerbated because inbreeding occurred nonrandomly with respect to f . Such tests require the set

Table 4: Relationships between an individual song sparrow's inbreeding coefficient (f) and the kinship difference (k_d) between the individual's observed mate and the set of all possible mates under the all-mates and new-mates null models across all females and males that paired on Mandarte during 1990–2004

	Females					Males				
	<i>N</i>	All-mates model		New-mates model		<i>N</i>	All-mates model		New-mates model	
		<i>F</i>	<i>P</i> (η^2)	<i>F</i>	<i>P</i> (η^2)		<i>F</i>	<i>P</i> (η^2)	<i>F</i>	<i>P</i> (η^2)
f	330	2.9	.09 (<.01)	2.3	.13 (<.01)	345	4.7	.031 (.01)	8.2	.026 (.01)
Year		1.0	.44	.8	.68		.8	.69	.9	.53
Year \times f		2.5	.002 (.09)	2.2	.008 (.09)		.9	.51	1.0	.45

Note: Values of η^2 for main and significant interactive effects of f are shown in parentheses.

of potential mates available to any individual to be known precisely. Furthermore, EPFs occur on Mandarte (O'Connor et al. 2006), introducing error into estimates of f and k . Since there is no evidence that EPFs occur systematically with respect to f and k (O'Connor et al. 2006), these EPFs should not bias analyses of mating patterns. Paternity error will, however, reduce power to detect nonrandom mating (Keller and Arcese 1998). Despite these limitations, analyses based on two null models of mate availability suggested that more inbred males paired with more closely related females than expected by chance. Similar trends were observed for females, but effect sizes were small and not statistically significant after we controlled for year. Immigrant song sparrows tended to pair with relatively outbred mates, although analyses were influenced by one outlying pairing. Overall, these patterns suggest that observed parent f –offspring f correlations may have been exacerbated by nonrandom inbreeding with respect to f . However, since f explained a small proportion of variation in k_d , any such effect is likely to have been small compared to the intrinsic parent f –offspring f correlation resulting from the population's relatedness structure. Nonrandom inbreeding could arise if inbreeding depresses the ability to recognize kin or because families of inbred relatives experience similar constraints on mate choice, perhaps reflecting their own poor condition (and therefore attractiveness, competitiveness, or timing of breeding). Further characterization of individuals that pair with close relatives is warranted on Mandarte and in other natural populations.

The suggestion that inbreeding occurs nonrandomly with respect to f , at least in males, does not contradict previous analyses that provided no evidence of overall inbreeding avoidance in song sparrows on Mandarte (Keller and Arcese 1998). Analyses designed to test for inbreeding avoidance across entire populations (e.g., van Tienderen and van Noordwijk 1988; Keller and Arcese 1998) may not detect subtle patterns of state-dependent avoidance, where some individuals avoid inbreeding while other individuals mate with close relatives. Future studies could

usefully test for inbreeding avoidance at the level of individuals rather than populations.

Mitton et al. (1993) showed that heterozygous parents produce a greater proportion of heterozygous offspring than do homozygous parents at loci with asymmetrical allele frequencies, causing a parent–offspring correlation in average heterozygosity. The parent f –offspring f correlation we observed in song sparrows differs from this mechanism in that it is not a fixed genetic principle; in unstructured and randomly mating populations, outbred parents do not necessarily produce more outbred offspring than do inbred parents (Falconer and Mackay 1996). Rather, the parent f –offspring f correlation arose primarily as an intrinsic consequence of the relatedness structure of a finite population open to immigration. The observation that parent f –offspring f correlations can arise in this way, rather than necessarily requiring complex patterns of nonrandom inbreeding, raises the possibility that such correlations may occur relatively widely. The magnitude of correlations will depend on properties of the population in question, including population size, life history, and frequency of immigration; modeling is underway to examine the impact of variation in these parameters and to estimate likely effect sizes. Intuitively, strong parent f –offspring f correlations seem most likely in (meta-) populations where groups of relatively sedentary individuals are linked by occasional longer-distance dispersers and where subpopulations are to some degree genetically differentiated ($F_{st} > 0$). It is increasingly apparent that such small-scale genetic structure may be common in natural populations, particularly in fragmented or variable habitats or in species with strong social structure (e.g., Cothran et al. 1983; Pierny et al. 1998; Ingvarsson and Giles 1999; Stewart et al. 1999; Surridge et al. 1999; Coltman et al. 2003; Rueness et al. 2003; Postma and van Noordwijk 2005). To test predictions and assess the generality of the patterns observed in song sparrows, parent f –offspring f correlations must then be measured in a variety of populations. Few data are currently available, and most focus on heterozygosity measured at few loci rather than direct

estimates of f . Mitton et al. (1993) report parent-offspring correlations in allozyme heterozygosity in limber pines *Pinus flexilis* and domestic horses ($r_s = 0.45$ and 0.32 , respectively). These correlations were attributed to deterministic correlations in heterozygosity at specific loci but in fact exceeded the theoretical maximum that could result from that mechanism (Mitton et al. 1993). Interestingly, allozyme heterozygosity was correlated across mothers and offspring in a white-tailed deer population known to show small-scale genetic structure (*Odocoileus virginianus*; $r = 0.37$; Cothran et al. 1983). Microsatellite heterozygosity was correlated across parents and offspring in Seychelles warblers (*Acrocephalus sechellensis*; $r = 0.25$ – 0.30 ; Richardson et al. 2004). Parent f was correlated with offspring f in a laboratory population of zebra finches (*Taeniopygia guttata*; $r \approx 0.25$; T. R. Birkhead and J. M. Reid, unpublished data).

Since f is a nonadditive genetic quantity, the gradients of parent f –offspring f regressions cannot be interpreted as strict heritabilities (Falconer and Mackay 1996). However, such gradients do describe the magnitude of parent-offspring resemblance with respect to f . Effect sizes observed on Mandarte ($r \approx 0.24$ – 0.49) were large compared to those observed for life-history traits in other populations (Kruuk et al. 2000; McCleery et al. 2004). This degree of parent-offspring resemblance is likely to be biologically significant, with implications for interpretations of empirical data and key analyses in evolutionary ecology.

First, effects of f on an individual's own phenotype are widely known (Keller and Waller 2002). However, intergenerational effects of parental f on offspring phenotype have also been documented (Keller and Waller 2002; Reid et al. 2003; Richardson et al. 2004). It is valuable to distinguish the two, since phenotypic effects of individual versus parental genotype can have different evolutionary consequences (Wolf et al. 1998). However, empiricists do not always test simultaneously for phenotypic effects of both individual f and parental f . In populations where parent f and offspring f are correlated, apparent effects of individual f could be confounded by unmeasured covariation with parent f , and vice versa.

Second, since phenotypes frequently deteriorate with increasing f , parent f –offspring f correlations could inflate trait heritabilities (h^2) estimated from parent-offspring regression. Genetic dominance effects can clearly inflate heritabilities estimated from full-sibling regressions, since $r = h^2/2 + (V_D/4 + V_E)/V_P$ (where V_D , V_E , and V_P are the dominance, environmental, and total phenotypic variances, respectively; Falconer and Mackay 1996). Parent-offspring regression is often employed to minimize this problem because h^2 can be estimated independently of V_D (Falconer and Mackay 1996). However, h^2 estimated from parent-offspring regression can be inflated by common

environmental effects that shape the phenotypes of both generations (Falconer and Mackay 1996; Griffith et al. 1999; Kruuk 2004). Parent f –offspring f correlations could inflate h^2 in a similar way, at least for traits that show inbreeding depression in both parents and offspring. The degree of inflation is generally small, since parent f –offspring f correlations are often weak, and f often explains a small proportion of phenotypic variation in natural populations (Keller 1998; Kruuk et al. 2002). However, heritabilities of physiological and fitness traits, which can show severe inbreeding depression (deRose and Roff 1999; Kruuk et al. 2002; Reid et al. 2003), could conceivably be overestimated by a few percent, introducing significant error into estimated evolutionary responses. Simple simulations indicate that a heritability of 0.15 would be overestimated by 25% given the parent f –offspring f correlation and magnitude of inbreeding depression for fitness observed on Mandarte (see Keller 1998). It is therefore possible that correlated inbreeding effects may partly explain the common mismatch between observed selection and microevolutionary change (Merilä et al. 2001). This source of nonadditive genetic resemblance between parents and offspring would not be eliminated by standard cross-fostering experiments designed to distinguish additive genetic from environmental components of variance.

Third, nonadditive genetic effects are increasingly suggested to play a key role in driving and maintaining sexual selection (Mays and Hill 2004; Neff and Pitcher 2005). Choosy individuals have been suggested to preferentially mate with genetically dissimilar mates in order to produce heterozygous or outbred offspring (Mays and Hill 2004; Neff and Pitcher 2005). The intrinsic parent f –offspring f correlation observed in song sparrows suggests that in populations with a similar relatedness structure, individuals could produce relatively outbred offspring by choosing mates that are themselves outbred (rather than specifically dissimilar). This effectively constitutes choice for carriers of recent immigrant genes and therefore a high probability of genetic dissimilarity. Female choice for rare alleles has been suggested in house wrens (*Troglodytes aedon*; Masters et al. 2003). Since individual f and multilocus heterozygosity can be signaled by secondary sexual ornaments (Reid et al. 2005), this mechanism of choice for outbred offspring mediated by choice for outbred mates could partly resolve the apparent dichotomy between choice for elaborate ornamentation and choice for dissimilar alleles (Mays and Hill 2004). Furthermore, since choice for heterozygosity rather than additive “good genes” may reduce the rate at which genetic diversity is depleted (Irwin and Taylor 2000), the possibility that sexual selection for outbred mates that produce outbred offspring may be maintained in the absence of direct benefits deserves further consideration.

In summary, our observation of an intrinsic parent f -offspring f correlation in free-living song sparrows, driven largely by the population's relatedness structure, serves to emphasize that population structure and the genetic implications of immigration need to be considered in order to understand patterns of phenotypic and genetic change, selection, and evolution in natural populations (Sugg et al. 1996; Keller et al. 2001; Postma and van Noordwijk 2005).

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